

POWDERY MILDEW ON CUCURBITACEAE: IDENTITY, DISTRIBUTION, HOST RANGE AND SOURCES OF RESISTANCE

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Synopsis

The species of powdery mildew fungi recorded on cucurbits are reviewed and the value of several characteristics of the imperfect stage in distinguishing these species in the absence of the perithecia is considered. One hundred and fifty collections were made in New South Wales from a wide area and climatic range and on numerous commonly grown species, cultivars and plant introductions of *Citrullus*, *Cucumis* and *Cucurbita*. All field collections resembled the imperfect stage of *Sphaerotheca fuliginea* in having conidia which are borne in chains, have well-developed fibrosin bodies and which produce germ tubes, some of which are forked. These characters have occurred consistently in mildews identified as *S. fuliginea* on the basis of perithecial characteristics by several workers in several countries.

Before 1958 *Erysiphe cichoracearum* had generally been assumed to be the most common and widespread powdery mildew species on Cucurbitaceae, but recent reports and results of this investigation now indicate that a mildew resembling the imperfect stage of *S. fuliginea* is generally the more important species.

Cucurbita hundelliana and numerous cultivars and plant introductions of *Cucumis melo* and *C. sativus*, which have previously been reported to have resistance to a mildew referred to as *Erysiphe cichoracearum* in the U.S.A. and in other countries, were found to have resistance to the powdery mildew in New South Wales.

A list has been made of cultivars and plant introductions of *Cucumis melo*, *C. sativus* and *Cucurbita* spp. which have shown resistance and which are suitable for commercial production or use in breeding programmes.

INTRODUCTION

Six species of powdery mildew fungi are recorded on Cucurbitaceae in various parts of the world: *Erysiphe cichoracearum* DC. ex Mérat, *E. communis* (Wallr.) Link., *E. polygoni* (DC.) St.-Am., *E. polyphaga* Hammarlund, *Leveillula taurica* (Lev.) Arnaud and *Sphaerotheca fuliginea* (Schlecht. ex. Fr) Poll. There are also records of conidial powdery mildew fungi as *Oidium* sp. More than one species may occur in the same locality (Teterevnikova-Babayan and Simonyan, 1956) and on the same plant (Deckenbach and Koreneff, 1927).

The two species most commonly recorded are *E. cichoracearum* and *S. fuliginea* but, since they rarely produce perithecia on cucurbits and their imperfect forms have many similar features, the validity of most published records based on the conidial stage requires confirmation.

In the U.S.A. resistance of cultivars and plant introductions was specifically claimed to be to *E. cichoracearum*. No mention has been made of resistance to *S. fuliginea*. However, Bohn and Whitaker (1961) stated that 'it seems desirable that studies designed to determine the true identity or identities of *Oidium* stages of Erysiphaceae on cucurbits should be made.' They drew attention to the conflicting host range reports in the literature, the demonstration of strains with different temperature requirements which 'suggested that the relationships need clarification.'

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In New South Wales powdery mildew is common on rockmelon (muskmelon) (*Cucumis melo* L.), cucumber (*C. sativus* L.) pumpkin (*Cucurbita maxima* Duch.), marrow (*C. pepo* L.) and other related plants (Noble *et al.*, 1934). The fungus was referred to as *E. cichoracearum* in earlier publications, but more recently has been termed *Oidium* sp. (Anon., 1959), as only the imperfect stage has been collected.

In the late 1950's the most widely grown rockmelon cultivar, Powdery Mildew Resistant No. 45 (PMR 45), became severely affected by powdery mildew in the south western areas of the State (Anon., 1959). The cultivars PMR Nos. 5 and 6 were resistant in 1959 but were severely affected the next season in the same districts (Anon., 1960). The conidia of all collections of the fungus on PMR Nos. 5, 6 and 45 contained well-developed fibrosin bodies (Zopf, 1887; Blumer, 1933; Homma, 1937; Clare, 1958), which may be used as a characteristic for distinguishing *Erysiphe* and *Sphaerotheca*. Their presence suggested that the fungus was the imperfect stage of *S. fuliginea* and not *E. cichoracearum*.

A survey of powdery mildews on Cucurbitaceae in New South Wales was therefore carried out from 1963 to 1965 to determine the species present and to compare the disease reaction of cultivars and breeding lines grown both here and in other countries.

THE FUNGI—TAXONOMY

Perithecia

Six species of powdery mildews have been recorded on cucurbits in the perithecial stage. Most records are of *E. cichoracearum* and *S. fuliginea* and their distributions are given in Tables 1 and 2. *Erysiphe polygoni* was recorded on *Cucurbita pepo* in Poland by Schroeter (1893) and in Japan on three uncommon species by Homma (1937).

There are several records of perithecia of powdery mildews on cucurbits under the names *E. communis* and *E. polyphaga* (Berlese and Peglion, 1892; Hammarlund, 1945; Blumer, 1952). Both the taxonomy and nomenclature of these two fungi need further study (Junell, 1965; 1967). The records of *E. cichoracearum* in Table 1 include those of *E. polyphaga*.

Leveillula taurica was listed, together with *E. cichoracearum* and *S. fuliginea* on cucurbits in the U.S.S.R. by Gordeeva (1961) and by Tarr (1955) with *S. fuliginea* in the Sudan. Golovin (1956) refers to *Leveillula* on *Cucurbitaceae* in her detailed survey of the genus, in which she split *L. taurica* into species for each host family. She described *L. cucurbitarum* on cucumber, marrow and *Cucurbita* sp. in the U.S.S.R. but the description is invalid as no Latin diagnosis is given.

Imperfect Stage: Taxonomic Value of Characters of the Imperfect Stage in distinguishing Powdery Mildew Species

As the identification of genera of powdery mildew is based primarily on characters of the perithecia which are not always developed, the definition of characteristics which could be used for precise identification in the absence of the perfect stage would be of great value. Length and structure of conidiophores, presence or absence of well-developed fibrosin bodies in conidia, and the morphology of the germ tubes and appressoria, all appear to be suitable characteristics (Ballantyne, 1963; Clare, 1964). The presence or absence of mycelial appressoria and hyphal swellings also provide useful characters for distinguishing species.

Leveillula taurica is easily distinguished from other powdery mildews on cucurbits in having internal mycelium and *Oidiopsis*-type conidiophores. *E. polygoni* is the only mildew with a single matured spore at the end of the conidio-

TABLE 1
Records of perithecia of *Erysiphe cichoracearum* on Cucurbitaceae

Country	Reference	Remarks
AFRICA		
No records		
ASIA		
India	Butler and Bisby, 1931	On <i>Momordica balsamina</i> and <i>Trichosanthes dioeca</i> .
"	Rajendrau, 1965	On <i>Lagenaria vulgaris</i> .
"	Khan <i>et al.</i> , 1972	On <i>Coccinia cordifolia</i> .
Malaysia and Singapore	Thompson, 1933	On pumpkin.
AUSTRALASIA		
No records		
EUROPE		
Surrey, England	Salmon, 1900	On <i>Cucurbita pepo</i> .
France	Viennot-Bourgin, 1956	On <i>Cucumis melo</i> and <i>C. sativus</i> .
Berlin, Germany	Roder, 1937	On <i>Cucumis sativus</i> .
Sweden	Junell, 1967	Four of ten collections on <i>Cucumis sativus</i> and <i>Cucurbita pepo</i> showed perithecia.
NORTH AMERICA		
Nova Scotia, Canada	Herbarium spec. 1798c. Dominion Laboratory of Plant Pathology, Coll. D. Creelman 1951	On <i>Cucumis sativus</i> .
Massachusetts, U.S.A.	Humphries, 1893	In a greenhouse.
Washington State, U.S.A.	Randall and Menzies, 1956	Perithecia on two <i>Cucumis</i> introductions U.S.P.I. 179260 and 181910 after a light frost.
Wisconsin, U.S.A.	Reed, 1908	Perithecia were on squash, pumpkin and cucumber cotyledons in a greenhouse.
SOUTH AMERICA		
No records		
U.S.S.R.*		
†Armenia	Teterevnikova-Babayan and Simonyan, 1956	Perithecia commonly occurred in the lowlands but not in the mountains.
†Crimea	Deckenbach, 1924	Perithecia of <i>Sphaerotheca fuliginea</i> were predominant on squashes and marrows. <i>E. cichoracearum</i> was not recorded on melon.
† "	Deckenbach and Korenski, 1927	Perithecia of <i>E. cichoracearum</i> occurred on the upper surfaces and <i>S. fuliginea</i> on the lower surface of <i>Cucumis melo</i> .
†Volga Basin	Rodgin, 1936	On unspecified cucurbits.

* Because of the difficulty in accurately placing some U.S.S.R. records in either Europe or Asia, a separate category was used.

† Indicates records where perithecia of *E. cichoracearum* and *S. fuliginea* occur together.

TABLE 2
Records of perithecia of *Sphaerotheca fuliginea* on *Cucurbitaceae*

Country	Reference	Remarks
AFRICA		
Republic of Sudan	Tarr, 1955	Perithecia collected on three occasions on <i>Cucurbita pepo</i> .
"	Nour, 1959	On <i>Cucurbita pepo</i> .
ASIA		
India	Butler and Bisby, 1931	On <i>Lagenaria vulgaris</i> and <i>Cucurbita moschata</i> .
"	Sohi and Nayar, 1969	On <i>Cucurbita moschata</i> .
"	Khan and Khan, 1970	On certain cultivars of <i>Cucumis sativus</i> and <i>Lagenaria leucantha</i> .
"	Khan <i>et al.</i> , 1972	On <i>Cucurbita maxima</i> and <i>Lagenaria leucantha</i> .
Israel	Rayss, 1947	On <i>Cucumis sativus</i> and <i>Cucurbita pepo</i> .
Japan	Homma, 1937	On <i>Cucurbita moschata</i> var. <i>toonas</i> .
"	Uozumi and Yoshii, 1952	Perithecia were common in late autumn in Fukioka but were uncommon elsewhere.
Taiwan	Hashioka, 1937	Perithecia formed in winter in the laboratory.
"	Sawada, 1959	On <i>Cucurbita maxima</i> and <i>C. moschata</i> var. <i>toonas</i> .
AUSTRALASIA		
New Zealand	Dingley, 1959	On <i>Cucurbita pepo</i> .
EUROPE		
Greece	Zaracovitis, personal communication	The perithecia are commonly formed.
"	Pantidon, 1971	On <i>Cucumis sativus</i> and <i>Cucurbita pepo</i> .
Hungary	Nagy, 1970	On <i>Cucumis melo</i> .
Turin, Italy	Blumer, 1933	On <i>Cucurbita pepo</i> .
Herastrau, Romania	Savalescu, Tr. 1929	On <i>Cucurbita pepo</i> .
People's Republic	Herbarium mycologicum Romanium Exsiccata	
	Fasc. 1, No. 10,	
	Anon., 1965	
Wageningen, The Netherlands	Bremer <i>et al.</i> , 1947	On <i>Cucurbita pepo</i> , <i>Cucumis melo</i> and <i>Lagenaria vulgaris</i> .
Turkey		
NORTH AMERICA		
No records		
SOUTH AMERICA		
No records		
U.S.S.R.*		
†Armenia	Teterevnikova-Babayan and Simonyan, 1956	Perithecia commonly occurred in lowlands, but not in mountains.
Astrakhan	Szembel, 1926	On melon.
Caucasus	Poretzky, 1923	On melon, <i>Cucumis melo</i> .
†China	Deckenbach, 1924	Perithecia on <i>S. fuliginea</i> were predominant on squashes, marrows and melons.
†	Deckenbach and Koreneff, 1927	Perithecia of <i>Erysiphe cichoracearum</i> occurred on the upper surface and <i>S. fuliginea</i> on the lower surface of <i>Cucumis melo</i> .
Southern Russia	Jaczevski, 1904	On pumpkin. Perithecia were extremely rare.
†Volga Basin	Rodigin, 1936	On unspecified cucurbits.

* Because of the difficulty in accurately placing some U.S.S.R. records in either Europe or Asia, a separate category was used.
† Indicates records where perithecia of *E. cichoracearum* and *S. fuliginea* occur together.

phore. The only confusion likely is between *E. cichoracearum* and *S. fuliginea* which both have external mycelium and *Oidium*-type conidiophores with long chains of conidia.

Fibrosin bodies were first reported by Zopf (1887) in the conidia and conidiophores of *Podosphaera oxycanthae*. Foex (1912, 1925) and Bouwens (1927) considered that they were of value in distinguishing certain species and described them in more detail. Blumer (1933) considered that presence or absence of fibrosin bodies was probably of some value in distinguishing the oidial stages of *E. cichoracearum* and *S. fuliginea* on cucurbits. This was confirmed by Homma (1937) who described two forms, a granular form characteristic of *Erysiphe* and a form characteristic of *Sphaerotheca* which is either cylindrical or disc-, cone-, or truncated-cone shaped.

Clare (1958, 1964) recognised the significance of well-developed fibrosin bodies and used their presence or absence in distinguishing mildews on cucurbits and other hosts in south eastern Queensland. Several workers, including Uozumi and Yoshii (1952), Hashioka (1937), Sawada (1959), Dingley (1959) and personal communication and Nagy (1970), either describe or figure well-developed fibrosin bodies in cucurbit powdery mildews identified on perithecial characters as *S. fuliginea* from Japan, Taiwan, New Zealand, The Netherlands and Hungary respectively. Ellert (1966) reported that these structures were present in powdery mildews identified as *S. fuliginea* from perithecia on non-cucurbitaceous hosts.

Klika (1922) reported fibrosin bodies in numerous species including *E. cichoracearum*, *E. polygوني* and *S. humuli* but without specifying the type.

The shape of the germ tube was claimed to be characteristic of the species of powdery mildew by Hirata (1942, 1955) and later by Zaracovitis (1965). The germ tubes of *E. cichoracearum* were simple with inconspicuous appressoria, those of *E. polygوني* formed complex appressoria, and some but not all of the germ tubes of *S. fuliginea* were forked. Hashioka (1937), Boerema and Van Kesteren (1964) and Nagy (1970) reported forking of the germ tubes of *S. fuliginea* on cucurbits in Taiwan, The Netherlands and Hungary. Homma (1937) and Salmon (1900) figure the many-lobed appressoria of *E. polygوني* on other hosts.

Conidia of *E. cichoracearum*, *E. polygوني* and *S. fuliginea* have generally similar shape and size. However, some workers (Bouwens, 1924; Yarwood, 1957 and Nagy, 1970) consider that measurements of length and breadth are of value in distinguishing between these species. Details of conidial measurements recorded by other workers on cucurbits are given by Ballantyne (1971).

A species of *Oidium* resembling the imperfect stage of *S. fuliginea* in having long chains of conidia, well-developed fibrosin bodies and a proportion of forked germ tubes, has been recorded throughout Australia and in several overseas countries (Table 3). Only two records of an imperfect stage lacking well-developed fibrosin bodies and resembling *E. cichoracearum* in other ways have been reported. These were on *Momordica charantia* L. and *Sechium edule* Sw. in Hawaii (Raabe, 1966) and on several cucurbits in Hungary, where it occurred with *S. fuliginea* which was identified on perithecial characteristics (Nagy, 1970)

THE HOSTS

Powdery mildew is a serious disease of susceptible rockmelon cultivars in many countries, particularly in arid areas where large scale commercial production often takes place. It is usually less severe on pumpkins, marrows, squashes and cucumbers, although it can be a serious problem in glasshouse cucumbers in Europe, mainly because of continuous culture and very favourable conditions for development of the disease. Watermelon (*Citrullus lanatus* (Thunb.) Mansfeld var. *caffer* Mansfeld) is not often affected, but occasional severe outbreaks

occur. In New South Wales two common cucurbitaceous weeds, the prickly paddy melon (*Cucumis myriocarpus* Naud.) and the wild watermelon or camel melon (*Citrullus lanatus* var. *lanatus*) may also be affected.

Rockmelon

The primary gene centre of *Cucumis melo* is probably in tropical Africa, and well-developed secondary gene centres of cultivated melons are in India, Iran, southern U.S.S.R. and China.

Many powdery mildew resistant lines have been collected in Asia and Africa and extensive breeding for resistance has been carried out. Details are in the Appendix.

TABLE 3

Records of Oidium sp. resembling the imperfect stage of Sphaerotheca fuliginia

<i>Africa</i>					
South Africa	Gorter, 1966
<i>Asia</i>					
India	Jhooty, 1967
Israel	Rudich <i>et al.</i> , 1969
<i>Australasia</i>					
New South Wales, Australia	Ballantyne, 1963 ; Clare, 1964
Northern Territory, Australia	Ballantyne, unpublished data
Queensland, Australia	Clare, 1958, 1964
South Australia	Harrison, personal communication
Western Australia	McNish, 1967
<i>Europe</i>					
England	Zaracovitis, 1965
Greece	Zaracovitis, personal communication
The Netherlands	Boerema and Van Kesteren, 1964 Kooistra, 1968
<i>North America</i>					
California, U.S.A.	Yarwood and Gardiner, 1964 Paulus <i>et al.</i> , 1968 Bohn, personal communication
New York State, U.S.A.	Kable and Ballantyne, 1963 Schroeder and Provvidenti, 1968
Ohio, U.S.A.	Ellert, 1966
<i>South America</i>					
No records					

The most widely grown cultivar is Powdery Mildew Resistant No. 45 (PMR 45) which was released in California in 1936 (Jagger and Scott, 1937), and is still widely grown though it was affected by a new race (race 2) in 1938 (Jagger *et al.*, 1938a). It is reported to be resistant to at least some of the races of powdery mildew present in some of the Eastern States of the U.S.A. (Markarian and Harwood, 1967).

Five genes for powdery mildew resistance have been designated, Pm¹⁻⁵ (Jagger *et al.*, 1938b ; Whitaker and Pryor, 1942 ; Bohn, 1961 ; Bohn and Whitaker, 1964 ; Harwood and Markarian 1968a and b).

Cucumber

India is considered to have been the centre of origin of the cucumber (Leppik, 1966b). Many powdery mildew resistant collections have been made in India and Africa and some breeding for resistance has been carried out. Details are in the Appendix.

Inheritance of resistance has been shown to be complex (Smith, 1948 ; Kooistra, 1968 ; Shanmugasundaram *et al.*, 1971).

Cucurbita species

America, possibly Central America and southern Mexico is the centre of origin of the genus *Cucurbita* (Whitaker, 1956).

Powdery mildew resistance has been reported in *Cucurbita lundelliana* L. H. Bailey where it is controlled by a single dominant gene (Rhodes, 1959 ; 1964) and in *C. martinii* L. H. Bailey. Further details are in the Appendix.

Watermelon

The watermelon probably originated in tropical Africa (Whitaker and Davis, 1962). There are no published reports of varietal resistance to powdery mildew.

Many rockmelon and cucumber cultivars bred for resistance in one country also have resistance in other countries. Details are given in Table 4.

MATERIALS AND METHODS

One hundred and fifty collections of powdery mildew were made from a wide range of locations and climates and on numerous cucurbit species and cultivars.

The fungus was mounted in 3% aqueous potassium hydroxide for examination of fibrosin bodies and in tap water for examination of the conidiophore and measurement of 20 conidia.

Germ tubes were obtained by germinating conidia on strips of onion bulb epidermis according to the method of Hirata (personal communication). Epidermis was stripped from the adaxial surface of the swollen leaf base, immersed for three to five minutes in 80% ethanol and washed in running water for two hours. The strips were placed on a microscope slide with the cuticular surface uppermost and blotted to remove excess moisture. Conidia were dusted onto the strip and tap water was added with a dropper so that the strip floated. Early collections were checked only for presence or absence of forking, but as investigation proceeded the need for more precise data was recognised and the percentage of germ tubes showing forking in at least 500 germinating conidia was determined for later collections.

The specimens are filed in the Herbarium of the Biology Branch, Biological and Chemical Research Institute, Rydalmere (DAR). Permanent mounts of the germinated and fresh spores were not made as no method of preserving these in a satisfactory condition was known. Herbarium specimens of conidial powdery mildews deteriorate with age and whilst structures resembling fibrosin bodies were detected in herbarium specimens ten years old, they were faint and infrequent.

THE HOSTS

As considerable variation had previously been observed in the reaction to powdery mildew of commercial lines of powdery mildew-resistant rockmelon cultivars, seed of such cultivars was obtained from the original breeder wherever possible. Where commercial seed was used, lines of each resistant cultivar were obtained from two different seedsmen. Details of seed source are given by Ballantyne (1971).

During 1963, 53 lines of *Cucumis melo* were grown at Rydalmere near Sydney, New South Wales, in hills with eight plants of each line per hill. Where seed of some of the U.S. Plant Introductions was limited, no fewer than four plants of each line were grown.

TABLE 4
Powdery mildew reaction of cucumber and rockmelon cultivars in areas other than U.S.A. and New South Wales

Country	Fungus	References	Cultivars resistant
AFRICA			
Republic of Sudan	<i>S. fuliginea</i>	Tarr, 1952	Some unspecified resistant cultivars bred in the U.S.A. showed varying degrees of resistance.
South Africa	<i>Oidium</i> sp. resembling <i>S. fuliginea</i>	Smit, 1964 Gorter, 1966	Georgia 47 rockmelon (<i>Cucumis melo</i>). Imperial 45 rockmelon.
ASIA			
Israel	<i>Oidium</i> sp. resembling <i>S. fuliginea</i>	Rudich <i>et al.</i> , 1969	Several rockmelon cultivars bred from PMR 45, Seminole and Davis X sources of resistance were resistant in Israel until 1967 and then became moderately susceptible. The cultivar Jacumba remained unaffected.
Japan	<i>S. fuliginea</i>	Tamai <i>et al.</i> , 1962	Iyo I, a powdery mildew resistant rockmelon cultivar was selected from PMR 5 × Earl's Favourite.
AUSTRALASIA			
Victoria, Australia	<i>Oidium</i> sp. resembling <i>S. fuliginea</i>	Kefford <i>et al.</i> , 1958 Harrison, personal communication McNish, 1967	PMR 45, Rio Gold and Invader (syn. Georgia 47) resistant.
Western Australia			PMR 45, PMR 5, Rio Gold, Florigold and Florisun rockmelons, and Ashley, Stono and Palomar cucumbers.
EUROPE			
The Netherlands	<i>S. fuliginea</i>	Anon., 1965	Of several cucumbers, viz., Ashley and related cultivars, U.S.P.T. Nos. 200815 and 200818 which have resistance in the U.S.A., and Natsufushinari which has resistance in Japan, most had some resistance in The Netherlands.
Portugal	unknown	Mendonca and Rodriguez, 1966	PMR Nos. 5, 6, 45 and 88 rockmelons.
NORTH AMERICA			
Mexico	unknown	Munoz, 1965	Edisto rockmelon.
U.S.S.R. Bulgaria	<i>S. fuliginea</i>	Lozanov and Vitanov, 1970	Rockmelon cultivars Edisto and PMR 45 resistant and PMR 6 highly resistant.

During 1964, 36 lines of *C. melo*, and ten lines of *Cucurbita* species were grown. These lines included cultivars of *C. maxima*, *C. moschata* and *C. pepo*, the three *Cucurbita* species cultivated in New South Wales, and *C. lundelliana*.

In the 1963 season, the results were recorded as resistant or susceptible (except for one line) as the plants were either free from disease or severely affected.

In the 1964 season, disease ratings were recorded on the following scale and the time of fruit maturity noted. The results (Table 5) were recorded when the fruit first ripened.

R—Fully resistant ; no mildew seen.

R⁻—Resistant ; mildew on less than 5% of leaf surface.

MR—Moderately resistant ; mildew on 5–30% of the leaf surface.

S⁻—Susceptible ; mildew on more than 30% of leaf surface ; ripe fruit produced.

S—Fully susceptible ; mildew on more than 30% of leaf surface ; no ripe fruit produced.

Observations were also made on the powdery mildew reactions of various lines grown in small scale replicated and unreplicated trials at Griffith and Yanco in the Riverina district in the south west of New South Wales during 1964 and 1965 and at Rydalmere in 1966.

Limited cross-inoculation experiments were carried out by transferring mildew spores with a scalpel from french bean (*Phaseolus vulgaris* L.), cucumber, and noogoora burr (*Xanthium chinense* Mill.) on to rockmelon (cv. Bender's Surprise) plants raised under bell jars.

RESULTS

The fungi

The 150 collections on naturally-infected cucurbits from New South Wales showed conidial characteristics of *S. fuliginea*. The percentage of forking in 80 specimens varied between 5 and 60%, with most specimens in the range 3 to 5%. Seventy specimens were checked only for presence or absence of forking. The conidial measurements were (24) 27–40 × 16–24 (27) μm.

The host plants on which mildew collected included : *Citrullus lanatus* var. *lanatus*, wild watermelon ; *C. lanatus* var. *caffer*, watermelon, one cv. ; *Cucumis melo* subspecies *conomon* (Thunb.) Greb., oriental pickling melon, eight accessions ; *C. melo* subspecies *melo*, cultivated rockmelon, 17 cvs ; *C. melo* subspecies and cultivar unknown, three accessions ; *C. myriocarpus*, prickly paddy melon ; *C. sativus*, cucumber, 11 cvs ; *Cucurbita ficifolia* Bouché, fig leaf gourd ; *C. lundelliana*, the peten gourd ; *C. martinexii* ; *C. maxima*, pumpkin and hubbard squash, 7 cvs ; *C. moschata* Duch. ex Poir, gramma, pumpkin and trombone, 2 cvs ; *C. palmata* Wats. ; *C. pepo*, marrow and squash, 5 cvs ; *C. radicans* Naud. ; *C. texana* A Gray ; *Cucurbita* spp. unknown and a gourd, genus and species unknown.

Most of the specimens were collected in February (78), March (24), January (22) and April (16), with less in May (5), June (3), July (1) and October (1). Ninety-four of the specimens were collected in the Sydney Metropolitan Area, 29 in the Riverina, 7 in the Central Tablelands, 4 in the North West Slopes, 5 in the Northern Tablelands, 3 each in the Manning and Central Coast area, 2 each in the Australian Capital Territory and on the North Coast and one in the North West Plains. One collection from the Northern Territory was examined. This specimen resembled those in the New South Wales area in having long chains of conidia, a similar size, well-developed fibrosin bodies and a proportion of forked germ tubes.

Both a collection from cucumber and a collection from french bean which resembled the cucurbit powdery mildew fungus, readily infected rockmelon plants in inoculation tests. A collection of powdery mildew on noogoora burr which differed from the cucurbit powdery mildews also infected rockmelon plants in an inoculation test. The collection showed the same characteristics on both the noogoora burr and the rockmelon: the conidia were borne in chains, lacked well-developed fibrosin bodies and produced simple unforked germ tubes. However, it grew sparsely on the rockmelon and soon died. Many of the spores of this fungus produced germ tubes from the end of the conidium whereas in other collections from cucurbits the germ tube usually grew from the side of the conidium.

Details of some representative collections are given below. Full details are given by Ballantyne (1971).

Conidial collections

Citrullus lanatus var. *caffer*, watermelon cv. Blacklee, Rydalmere glasshouse, March, 1963, DAR 7954, B. Ballantyne;

Cucumis melo subspecies *conomon*, oriental pickling melon, C* 46, (U.S.P.I. 157070, L† 90128), Rydalmere, February, 1963, DAR 7914, B. Ballantyne;

C. melo subspecies *melo*, rockmelon (muskmelon) cv. PMR 45, Yoogali, February, 1963, DAR 7984, B. Ballantyne.

C. sativus, cucumber cv. Polaris, Duranbah, October 1963, DAR 12226, F. Autry Hall;

Cucurbita moschata, pumpkin cv. Butternut, C153, Eastwood, February 1964, DAR 12801, B. Ballantyne.

Perithecial collections

Erysiphe cichoracearum. On *Cucumis sativus*, 1951, Dominion Laboratory of Plant Pathology, KP 1798c, KP 1798d, Nova Scotia, Canada, D. Creelman.

Sphaerotheca fuliginea. On *Cucurbita pepo*, 1925, Herbarium mycologicum Romanicum Exsicatti Fasc. 1, No. 19, Herastrau, Romania People's Republic, Tr. Savalescu (ex CUP).

THE HOSTS

Disease reactions as reported in the U.S.A. and observed in New South Wales are given in Table 5.

Rockmelon. In 1963 at Rydalmere, the cultivars Delta Gold, Edisto, PMR Nos. 6, 45 and 88, Rio Gold, Seminole and U.S.P.I. Nos. 124111, 124112 and subline L90209 of 183310 showed no signs of mildew. Other cultivars and U.S.P.I. Nos. were severely affected.

In 1964 at Rydalmere, PMR Nos. 6 and 88, Seminole, LJ 430, breeding lines 151, 157 and 180 of M. B. Hughes, the P. lines (2-9, 10) of G. W. Bohn and U.S.P.I. 234607 were fully resistant. Delta Gold, Edisto, PMR 45, Rio Gold and Wescan were resistant. United States P.I. Nos. 164756, 165525 and 183307 gave mixed reactions with some resistant, some moderately resistant and others susceptible. Florida No. 1 was moderately resistant, Florisun, Floridew and U.S.P.I. 134200 were susceptible and other cultivars were fully susceptible.

In 1964 at Griffith, PMR Nos. 6 and 88, Seminole, 151, 157, 180, LJ 430 and the P lines were fully resistant and PMR 45 and Edisto were fully susceptible. In 1965 at Griffith the same results were obtained except that the P lines were not included. In 1966 at Rydalmere, Campo and Jacumba were fully resistant.

* indicates the accession number of the authors collection.

† indicates the numbers given by the U.S. Horticultural Field Station, La Jolla, which provided seed of such lines.

TABLE 5
Reaction to powdery mildew of lines of Cucumis melo in the U.S.A. and in New South Wales

Line	United States of America		New South Wales	
	California and Texas	Eastern States	Rydalmere	Riverina
	Reaction Reference	Reaction Reference	Reaction	Reaction
Group A—cultivars and lines with resistance from one or more of the genes Pm ¹ , Pm ² and Pm ³ . Full details of parentage are in Ballantyne, 1971.				
PMR 45	*S Jagger <i>et al.</i> , 1938 *R	Markarian and Harwood, 1967	†R 1963, 1964	†S 1959†
PMR 6	*R Pryor <i>et al.</i> , 1946 *R	"	†R 1963, 1964	*R 1959 Anon., 1959 *S 1960 Anon., 1960 †R 1963, 1964, 1965
Wesau	*MR Anon., 1963		†R—1964	
U.S.P.L. 124111	*R Pryor <i>et al.</i> , 1946		†R 1963	*R 1961 Sumeghy, personal communication
LJ 430	*R Bohn, personal communication		†R 1964	†R 1964, 1965
Campo	*R Bohn <i>et al.</i> , 1965	Markarian and Harwood, 1967	†R 1966	
Jacumba	*R "		†R 1966	
PMR 88	*R Bohn, 1958		†R 1963, 1964	†R 1964, 1965
P2-P8 P10 8 lines	*R Bohn, 1961		†R 1964	†R 1964

TABLE 5—Continued
Reaction to powdery mildew of lines of *Cucumis melo* in the U.S.A. and in New South Wales

Line	United States of America		New South Wales	
	California and Texas	Eastern States	Rydalmere	Riverina
	Reaction Reference	Reaction Reference	Reaction	Reaction
Group B—cultivars and lines with resistance most likely governed by one or more of the genes Pm ⁴ and Pm ⁵ .				
U.S.P.I. 124112 4 lines	*R Pryor <i>et al.</i> , 1946		†R 1963	*R 1961 Stumegly, personal communication
Seminole	*MR Bohn, personal communication	*R Whitner, 1960 Markarian and Harwood, 1967	†R 1963, 1964	†R 1963, 1964, 1965
Delta Gold	*R	Brown <i>et al.</i> , 1960	†R 1963 †R-1964	†R-1962†, 1963†
Florida No. 1	*MR	Jamison <i>et al.</i> , 1963	†MR 1964	
151	*R	Hughes, personal communication	†R 1964	†R 1964, 1965
157				
180				
Group C—cultivars and lines with resistance from genes which have not been identified or designated.				
Rio Gold	*S Correa, personal communication	*R Epps, 1956 Kelbert, 1956 Whitner, 1956	†R 1963 †R-1964	
Edisto	*S Bohn, personal communication	*R 1957 Hughes, personal communication *S 1958†	†R 1963 †R-1964	†S 1964
Florisan	*MR *very low level resistance	Jamison <i>et al.</i> , 1963 Markarian and Harwood, 1968b	†S-1964	

Continued overleaf

TABLE 5—Continued
 Reaction to powdery mildew of lines of *Cucumis melo* in the U.S.A. and in New South Wales

Line	United States of America		New South Wales	
	California and Texas	Eastern States	Rydalmere	Riverina
	Reaction Reference	Reaction Reference	Reaction	Reaction
Florida				
	*MR *very low level resistance	Jamison <i>et al.</i> , 1962 Markarian and Harwood, 1968b	†S- 1964	
U.S.P.I. 134200	*R Pryor <i>et al.</i> , 1946	*S Mortensen, personal communication	†S- 1964	
U.S.P.I. 164756§	*R	Mortensen, 1961	†7 R 1964 †1 S	
U.S.P.I. 165525	*R	Mortensen, 1961	†7 R 1964 †1 MR	
U.S.P.I. 183307	*R Langford and Killinger, 1961	Mortensen, 1961	†1 R 1964 †2 MR †5 S	
U.S.P.I. 183310 90209 90211	*S Whitaker, personal communication " "		†R 1963	*R 1961
U.S.P.I. 234607	*R	Mortensen, personal communication	†R 1964	*S 1961 Stumeghy, personal communication

* denotes results reported by other workers.

† denotes results of the author.

R = Resistant

MR = Moderately resistant

S = Susceptible

‡ observations made on commercial plantings.

§ Lines from open-pollinated fruit.

Exact description of these terms as used in this work is on p. 108.

Cucumber. In 1964 at Rydalmere, Pixie and Polaris were resistant, Ashley, Palomar and Stono were moderately resistant, U.S.P.I. 197087 gave a mixed reaction with two plants moderately resistant and the other two susceptible. This plant introduction was probably not a pure line (Barnes, personal communication). Other cultivars and U.S.P.I. Nos. were susceptible including 179260 and 181910 (probably not pure lines [Bohn, personal communication]) on which Randall and Menzies (1956) recorded perithecia of *E. cichoracearum* in the U.S.A. No perithecia of any mildew fungus were seen on these introductions in this trial or on any other cucurbit host in New South Wales.

Cucurbita species. In 1964 at Rydalmere two plants of *C. lundelliana* which produced mature fruit were moderately resistant, one which did not produce mature fruit was resistant and the fourth was fully resistant. Other cultivars of *C. maxima*, *C. moschata* and *C. pepo* were susceptible.

DISCUSSION

Considerable confusion has arisen in the literature because the name of the perfect stage of a powdery mildew fungus has so commonly been given to the imperfect stage without adequate identification. There is no doubt that both *E. cichoracearum* and *S. fuliginea* can occur on cucurbits in several countries, e.g. India and the U.S.S.R., because perithecia of these two fungi have been recorded on several occasions.

Before 1958 *E. cichoracearum* had generally been assumed to be the most common and widespread powdery mildew species reported on Cucurbitaceae. However, this investigation and recent reports from many countries indicate that a mildew having major features of the imperfect stage of *S. fuliginea* is the predominant mildew in some countries, and probably the only species in others. Only two instances of an imperfect stage resembling *E. cichoracearum* have been reported on cucurbits. One was in Hawaii on *Momordica charantia* and *Sechium edule*. The other was in Hungary where two powdery mildews commonly occur on cucurbits; one identified as *S. fuliginea* from perithecia, and the other identified as *E. cichoracearum* on conidial characteristics (Nagy, 1970).

All naturally infected collections of cucurbit powdery mildew from many areas and a wide range of climates in New South Wales resembled the imperfect stage of *S. fuliginea*. The poor vigour of the mildew resembling *E. cichoracearum* from noogoora burr when artificially inoculated on to rockmelon suggests that this fungus is not important on cucurbits in the field in New South Wales.

Observations by many investigators support the contention that the type of conidiophore, the presence or absence of well-developed fibrosin bodies and the mode of germination are useful criteria for distinguishing between the powdery mildew species recorded on cucurbits. The very consistent data obtained in the present study also support this. The reliability of these characters could be further checked by culturing these species from ascospores under controlled conditions and examining the colonies. In addition, characters which would permit mixtures of species to be detected would be valuable if these could be found. The conidial dimensions of *E. cichoracearum*, *E. polygoni* and *S. fuliginea* have generally been considered to be too similar to be of value in distinguishing these species. Nagy (1970) compared length: width ratios of two cucurbit powdery mildew fungi in Hungary; one was identified as *S. fuliginea* on the basis of perithecial characteristics and the other as *E. cichoracearum* from the morphology of the conidia. He found that the length: width ratio was significantly different for the two species. However, he only quoted mean measurements for length, width and the ratio between. The range of measurements of 50 conidia was not given.

It is considered that the mildew present on naturally infected cucurbits in New South Wales is the imperfect stage of *S. fuliginea*.

Many cultivars, breeding lines and plant introductions of several species of cucurbits with reported resistance to *E. cichoracearum* were shown to have resistance to a fungus resembling *S. fuliginea* in this investigation.

Tables 4 and 5 show that there is generally a close similarity in powdery mildew reaction in different countries of various species and cultivars with different genes and sources of resistance. An exception is in the reports of Kooistra (1968), who found only slight resistance in many of the cucumber lines reported to have a higher degree of resistance in other countries. However, his testing was carried out under glasshouse conditions which are very favourable for powdery mildew development and in which reactions cannot be regarded as typical of field behaviour. Leppik (1966*a*) reported that some lines with good resistance in the field showed less resistance under glasshouse conditions.

Some cultivars have a long history of resistance whereas others have resistance when first grown and are later affected by another race of the fungus. For example, the rockmelon cultivar PMR 45, whose resistance is due to the single dominant gene Pm¹, was resistant when first grown in California, New South Wales and Israel but later was affected by a new race in these three areas. There have been no reports of the disease affecting cultivars such as Campo and Jacumba, whose resistance may be derived from several genes including one from U.S.P.I. 124111. Where breeding programmes are being initiated or new sources of resistance are being introduced into existing programmes, preference should be given to lines having a history of resistance in several areas, including some where races capable of severely affecting a range of cultivars are present. The race 2 which occurs in California and Texas appears to be similar to the race which occurs in south western New South Wales, except that the rockmelon cultivar Seminole, which has shown no sign of mildew here, is only moderately resistant in California. It is likely that the races designated 1 and 2 are both complexes of races.

The severe outbreak of powdery mildew on the cultivar PMR 6 in the 1960 season and its resistance in the 1959, 1963, 1964 and 1965 seasons could be due to the disappearance of the PMR 6—attacking form at the end of the 1960 season. The conidia are short-lived and winter conditions in inland and southern coastal New South Wales are too cold for survival of cucurbits. Perithecia have not been found despite thorough search and overwintering on some other host is therefore considered to be the likely means of survival. Alcorn (1967, 1969) found seven non-cucurbit genera were alternative hosts of the cucurbit powdery mildew fungus in Queensland, but these are sub-tropical or tropical species and do not survive winter conditions in southern New South Wales.

Perithecia of powdery mildew fungi occur commonly in some countries and rarely or not at all in others. Perithecia of numerous powdery mildew species occur frequently in the Northern Hemisphere (Salmon, 1900; Blumer, 1933; Viennot-Bourgin, 1956; Junell, 1967; Saville, 1968 and Solheim, *Mycoflora Saximont. Exsicc. various Nos. in Herb. DAR*), but perithecia of very few species have been recorded in Australia.

Heterothallism is a possible explanation of perithecia being common in some areas and rare or lacking in others. They may be more common in the centre of origin of the species and rare or lacking in other areas where only one mating type of fungus was introduced.

Perithecial formation is more frequent on some host species and cultivars than others (Yarwood, 1957; Khan and Khan, 1970; Price, 1970). Most records of *S. fuliginea* and *E. cichoracearum* have occurred on *Cucumis sativus* and *Cucurbita pepo* (Tables 1 and 2). Alcorn (1969) distinguished at least four patho-

genically distinct races of the cucurbit powdery mildew resembling *S. fuliginea* in Queensland, all of which infected *Cucumis sativus*, *Cucurbita maxima* and *C. pepo*, but not all infected the two cultivars of *Cucumis melo* and the single cultivar of *Citrullus lanatus* var. *caffer* onto which they were inoculated. Perithecia may occur on particular hosts such as *Cucumis sativus* and *Cucurbita pepo* more often because these are susceptible to a wider range of isolates. The probability of opposite mating types occurring together is therefore greater. More widespread culture of these two species could also be the reason.

Homma (1937) reported that heterothallic species seemed to be more common than homothallic ones in Japan. She showed that an isolate which she identified as *S. fuliginea* on *Taraxacum ceratophorum* DC. was homothallic. However this isolate has smaller than typical conidial and perithecial stages and may be a different species.

Smith (1970) reported heterothallism in four mildew species in England and suggested that any lateness or irregularity in perithecial formation in the field is due to absence of the necessary mating types rather than to an unfavourable environment or the nutritive condition of the host.

One might expect to find resistance in areas where both the pathogen and host have been evolving side by side. Most of the powdery mildew resistant collections of *Cucumis* have been made in the primary, secondary and tertiary gene centres of this genus in Africa, India and nearby Asian areas, where the imperfect stage of the mildew resembles *S. fuliginea* and perithecia of this fungus have been recorded on several occasions. Perithecia of *E. cichoracearum*, which is heterothallic (Morrison, 1961), have also been recorded on cucurbits in some of these countries.

Many powdery mildew-resistant lines of *Cucumis* have been recorded but little resistance has been reported in *Cucurbita*. This could be explained by the presence or absence of powdery mildew in the gene centres in the early stages of evolution of these genera. It is likely that *S. fuliginea* has been present in Africa, India and nearby Asian areas for very long periods of time, as suggested by the occurrence of perithecia. This would have favoured selection of mildew resistance in *Cucumis*. No perithecia of *S. fuliginea* have been recorded on cucurbits in the Americas, although they have been found on other hosts. A mildew resembling the imperfect stage of *S. fuliginea* is common and widespread on cucurbits in North America.

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APPENDIX

POWDERY MILDEW RESISTANT COLLECTIONS AND CULTIVARS

Rockmelon (*Cucumis melo* L.)

Many plant introductions have been collected from Asia, Europe and Africa. Several workers (Pryor *et al.*, 1946 ; Mortensen, 1961, 1962 and personal communication ; Leppik, 1966a ; Corley, 1966 and Oda, 1969) have reported on the reaction of some of these to powdery mildew. Of 202 introductions from Asia, Europe and Africa for which disease resistance was given in Corley's compilation, 56 were resistant to powdery mildew in the U.S.A. Most of these were from India (49) with others from Turkey (2), Africa (1), Iran (1), Peru (1), Saudi

Arabia (1) and the origin of one was not listed. Leppik (1966*a*) reported an additional five resistant introductions from India. Oda (1969) reported four introductions from India and one from Burma had a very high level of resistance to powdery mildew, six from India and one from Nepal had intermediate resistance and three others from India had a low level of resistance.

Resistant Cultivars

Cultivars bred in California and Texas for resistance to race 2 are PMR Nos. 5, 6 and 7 (Pryor *et al.*, 1946), PMR 88 (Bohn, 1958), Wescan (Anon., 1963), Perlita (Anon., 1964), Campo, Jacumba (Bohn *et al.*, 1965), Dulce (Anon., 1969*a*) and Tam-dew (Anon., 1971). Those bred elsewhere in the U.S.A. for powdery mildew-resistance include Georgia 47 (Minges, 1972), Delta Gold (Brown *et al.*, 1960), Seminole (Whitner, 1960), Floridew, Florida No. 1, Florisun (Jamison *et al.*, 1962; 1963), Golden Perfection (Brasher, 1965), Gulfstream (Minges, 1972), Southland (Norton, 1970) and Gulfcoast (Norton, 1971).

Cultivars bred or selected for resistance in other countries are: in Israel, Yokniam 54 and 56 (Ilan, 1963) and Ananas PMR, Pearl of En Dor, Yellow Honeydew E1313 and Green Honeydew E3412 bred with PMR 45, Seminole and Davis X as sources of resistance (Rudich *et al.*, 1969); in Japan, Iyo 1 bred from PMR 5 and Earl's Favourite (Tamai *et al.*, 1962); and in New South Wales, Yanco Treat and Yanco Delight bred from subline 36739 of U.S.P.I. 124111 (Anon., 1969*b*).

Cucumber (*Cucumis sativus* L.)

Powdery mildew resistant collections have been made from Burma, U.S.P.I. Nos. 200815 and 200818 (Wilson *et al.*, 1956); from Japan, U.S.P.I. 279465 and from Ethiopia, U.S.P.I. 233646 (Leppik, 1966*a*), from India, U.S.P.I. 197087 (Barnes, 1961) and from China, several varieties including Vladivostoksky 155, Di-huan-guas and Ty-hy-cy (Mescherov, 1961) and Puerto Rico Nos. 37 and 40 (Roque and Adsuar, 1939; Smith, 1949). Leppik (1966*b*) reported that several wild cucumbers from India were immune and several wild species from Africa were resistant to powdery mildew but they could not be crossed easily with cultivated cucumber.

Resistant Cultivars

Resistance to powdery mildew has been reported in the following cucumbers bred in the U.S.A.: Ashley, Stono and Palomar, three cultivars whose resistance appears to be derived from Puerto Rico 40 (Barnes and Epps, 1956); Polaris, Pixie, Pointsett and Cherokee, four cultivars whose resistance appears to be derived from U.S.P.I. 197087 (Barnes, 1961; Minges, 1972) and Tablegreen, whose source of resistance is unknown (Minges, 1972). The cultivar Natsufushinari is reported to be resistant to powdery mildew in Japan (Hujieda and Akija, 1962) and Fävor is listed as resistant to the disease in Sweden (Banga, 1956).

Cucurbita species

Cucurbita lundelliana L. H. Bailey, the peten gourd, which is cross compatible with the cultivated species of *Cucurbita* (*C. maxima* Duch., *C. moschata* Duch. ex Poir. *C. mixta* Pang. and *C. pepo* L.) has resistance to powdery mildew in the U.S.A. (Whitaker, 1956). Rhodes (1959) developed a gene pool among these species and recovered hybrid plants tolerant to powdery mildew. Whitaker (1965) developed relatively stable lines from crosses involving *C. moschata* and *C. pepo* with *C. lundelliana*. These lines have a higher degree of resistance than the susceptible commercial cultivars. Bemis (personal communication) reported that *C. martinensis* L. H. Bailey has powdery mildew resistance similar to *C. lundelliana*.